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SUMMARY AND CONCLUSIONS

1. Chronically implanted microelectrode wires in the L₇ and S₁ dorsal root ganglia were used to record unit activity from cat hindlimb primary and secondary muscle spindle afferents. Units could be reliably recorded for several days, permitting comparison of their activity with homonymous muscle EMG and length during a variety of normal, unrestrained movements.

2. The general observation was that among both primary and secondary endings there was a broad range of different patterns of activity depending on the type of muscle involved and the type of movement performed.

3. During walking, the activity of a given spindle primary was usually consistent among similar step cycles. However, the activity was usually poorly correlated with absolute muscle length, apparently unrelated to velocity of muscle stretch, and could change markedly for similar movements performed under different conditions.

4. Spindle activity modulation not apparently related to muscle length changes was assumed to be influenced by fusimotor activity. In certain muscles, this presumption leads to the conclusion that gamma-motoneurons may be activated out of phase with homonymous alpha-motoneurons as well as by more conventional alpha-gamma-motoneuron coactivation.

5. Simultaneous recordings of two spindle primary afferents from extensor digitorum longus indicated that spindles within the same muscle may differ considerably with respect to this presumed gamma-motoneuron drive.

6. Spindle secondary endings appeared to be predominantly passive indicators of muscle length during walking, but could demonstrate apparently strong fusimotor modulation during other motor activities such as postural changes and paw shaking.

7. Both primary and secondary endings were observed to undergo very rapid modulation of firing rates in response to presumed reflexly induced intrafusal contractions.

8. It is suggested that the pattern of fusimotor control of spindles may be tailored to the specific muscle and task being performed, rather than necessarily dominated by rigid alpha-gamma coactivation.

INTRODUCTION

Any hypotheses as to function(s) of the muscle spindle afferents must include hypotheses as to the role(s) of efferent gamma-motoneurons, which can greatly modify receptor properties (18) and modulate spindle afferent discharge during movement (34). Coactivation of alpha- and gamma-motoneurons to ankle extensors and flexors has been demonstrated during locomotion in decerebrate cats (35) and in spinalized cats given dopa and deafferented or paralyzed (36). Vallbo (40, 41) has demonstrated alpha-gamma coactivation under more normal but restricted movements. However, it remains unclear whether and to what extent fusimotor activity always mimics the homonymous extrafusal activity.

Recently, Prochazka et al. (31, 32) have obtained short-term recordings from Ia (spindle primary) afferents from ankle extensors and hamstring muscles during normal, unrestrained walking, and have found

much less apparent alpha-gamma coactivation than seen in decerebrate cats. This latter is in agreement with data from jaw muscle spindles in cats (39) and monkeys (26), but conflicts with records in humans from spindle afferents in forearm muscles during fine control movements where strong coactivation appears to occur (40, 41). This discrepancy suggests that there may be differences in spindle behavior depending on the type of muscle and movement involved.

Using a new technique (24), we have been able to obtain recordings of activity from both spindle primary and spindle secondary endings in intact, unrestrained cats, and to maintain stable single-unit records for several days. This stability facilitated identification and study of spindle afferents from some of the smaller muscles providing fine control and stabilization of the hindlimb, and allowed time to implant some specific muscles with EMG electrodes and length gauges to provide a basis for correlating afferent activity with electromechanical events in the parent muscles under a variety of spontaneous and reflexly evoked movements. Our floating-microelectrode technique is similar to that developed independently by Prochazka et al. (31), but in recording from cell bodies in the dorsal root ganglia (DRG) rather than from dorsal root fibers, we have found both much less bias in favor of the largest myelinated fibers and much greater stability of unit recording.

A disadvantage shared by both techniques is inability to move the electrodes implanted among the neurons to sample units for systematic study, making it difficult to acquire large samples of afferents from a given muscle under homogeneous conditions. We have chosen to present what are, so far, essentially "anecdotal" examples of muscle spindle behavior because we believe each to be a well-documented description of a normal physiological event for which any valid, comprehensive theory of motor control must account.

METHODS

Surgical techniques

DRG FLOATING MICROELECTRODES. The afferent unit records were obtained from flexible insulated wires implanted in the L₇ and S₁ DRG of seven adult male cats using a procedure de-

scribed previously (24). Under pentobarbital anesthesia and sterile conditions, a dorsal midline incision from L₆ to S₁ was used to expose the L₇ vertebral lamina, and a small burr hole through the lamina at the base of the dorsal spinous process exposed both ganglia extradurally. A bundle of 10 electrode wires (50- μ m diameter platinum-10% iridium alloy with Pyre-TML insulation, California Fine Wire Co., plus 12 μ m Parylene-C insulation) carried in an electrically shielded flexible silicone rubber sleeve was anchored to the dorsal spine. The wires were cut obliquely to expose the ends and inserted by forceps into the DRG, leaving small loops of slack wire. The incision was closed bringing the silicone rubber sleeve up through another anchoring point at the outer fascial layer and into a semiflexible rubber saddle, which was sutured to the fascia through the skin adjacent to the laminotomy wound. The microelectrode leads plus a ground wire and EMG and length-gauge leads passed subcutaneously from devices described below were soldered to multipin connectors permanently mounted in the saddle. The animals tolerated both the surgery and the saddle well and were able to walk normally in 1-2 days, displaying no discomfort when the saddle was manipulated to attach the preamplifiers.

LENGTH GAUGES. At the time of the laminotomy, the ipsilateral hindlimb was usually fitted with length gauges at the hip, knee, and ankle, using construction and fixation techniques discussed elsewhere (25). The gauges consisted of platinum electrodes fixed in the ends of distensible silicone rubber tubes, which were filled with hypertonic saline and sealed. The gauges were surgically tethered at their ends to bony landmarks on either side of a joint, and they sensed the length of the path (generally subcutaneous) between the insertion points using changes in the electrical resistance of the fluid column in the stretched tubing. Records shown here represent the rectified and integrated signal (100-Hz high cutoff) from a 20-kHz AC bridge for each gauge. Calibration was obtained for each record by measuring the actual angles traced from videotape stills (reflective dots were permanently glued to the skin to help identify skeletal landmarks). The frequency response (greater than 200 Hz) and linearity of the gauges have been described (25); they are generally better indicators of point-to-point lengths such as muscle length than joint angle, but they have been calibrated in degrees here to facilitate comparison with the kinesiological literature. Arrows indicate direction of increasing length for the muscle under discussion.

EMG ELECTRODES. A special technique was developed to insure reliable recording of EMG

from individual small muscles. A pair of stranded stainless steel wires with Teflon jackets (Bergen wire rope BWR 3.48) was prepared with approximately 1 mm exposed tips and were tied together near their tips with braided Mersilene suture so that the tips were offset 2–3 mm. At implantation, the swaged-on needle of the Mersilene suture was driven through the belly of the muscle and the suture used to drag the EMG electrode tips into the middle of the muscle. The two ends of the suture were tied loosely around the outside of the muscle and the leads passed subcutaneously to the saddle connector, taking care to leave ample slack at all positions of the limb. Such electrodes had 1- to 2-k Ω tip impedance (at 1 kHz) and always recorded large, multiunit EMG activity that was independent of activity in adjacent muscles. The placement of the electrodes was always confirmed at postmortem dissection. The records shown in this paper include both simple differential amplifier output and a Paynter filter integration (50 ms time constant, three-pole Butterworth design) of rectified EMG (17).

Experimental procedure

PROTOCOL. At the beginning of each postoperative day, the impedance of all microelectrodes and the presence or absence of neural units were determined. The animal was placed on a glass-enclosed treadmill and walked for several short periods at various speeds while the signals from the active electrodes and transducers were taped along with synchronization information for the videotape record. In some experiments, electrical stimuli were delivered during walking through previously implanted bipolar electrodes in muscles (also used for EMG) or subcutaneous sites (Digitimer D4030 with Devices type 2533 isolated stimulators). Various manipulations as described below were also performed. Stimuli were kept at nonnoxious levels to avoid generalized effects on gait.

The animal was then lightly anesthetized (ketamine) and the activity on each microelectrode examined individually to identify the amplitude and waveform of unit action potentials evoked by manipulation of the skin and joints. The units were further identified by receptor modality and proprioceptors were characterized by the battery of tests described below. When interesting new units were observed, minor surgical dissections were occasionally performed under aseptic conditions and additional anesthesia (Pentothal) to identify the precise origin of the unit and/or to implant additional EMG electrodes and length gauges, which were connected to unused saddle connector pins.

DATA COLLECTION. Although the DRG microelectrodes have relatively low impedance (150–250 k Ω at 1 kHz), it is desirable to further

reduce the signal impedance near the source before exposure to cross-talk and interference in connecting cables. A miniature 10-channel unity gain "backpack" preamplifier was plugged directly into the saddle connector to amplify the DRG microelectrode signals, which were then transmitted via flexible ribbon cable from the cat to custom-built high-gain amplifiers (1- to 10-kHz band pass). A separate ribbon cable carried unamplified EMG signals and length-gauge bridge signals from a second connector on the saddle to custom-built amplifiers.

Selected electrode and transducer signals were recorded on a 14-channel FM tape recorder (Hewlett-Packard 3955, DC, 10-kHz frequency response) along with a treadmill speed indicator and Irig-B time code from a Datum model 9300 timer synchronized to the video system. The cat's gait and other movements were recorded at 60 fields per second under normal room light by a Plumbicon short-persistence camera (Telemation TMC-1100). This video signal was combined with that from the timer display and recorded on a Sony VO-2800 1-inch cassette recorder equipped with a Convergence SM-2 variable-speed and single-field playback controller.

UNIT ANALYSIS. Microelectrode signals were separated into individual units (usually one to three per electrode at any one time) using a variable time-delay window discriminator (3). The entire waveform shape was obtained using an analog IC delay line (2) and recorded on Polaroid film from the face of a storage oscilloscope (Tektronix R5103N-D15) for immediate reference. Reidentification of previously recognized units was almost always easily made because of the distinctive and constant action-potential waveforms (24) (see Fig. 1D) and the large amount of easily obtained receptor characterization data for the unit and for others simultaneously present. This waveform identification plus consideration of firing pattern (e.g., physiological interspike-interval ranges) made it possible to identify reliably and isolate most units from the activity recorded during walking. Since the same amplifiers and discriminators were used during unit identification, gait recording, and data analysis, it was frequently our practice to play back part of the tape-recorded data during the unit characterization testing to confirm that the same window discriminator settings would separate one and only one unitary action-potential waveform.

In the records presented here, unprocessed electrode signals are given where the unit under discussion was the only or largest active one. More often, window discriminator acceptance pulses are shown as vertical ticks and/or instantaneous spike frequency (obtained on-line as the digital inverse of the preceding interspike interval). The latter are shown in bar diagrams with 10-ms hold periods, which facilitates apprecia-

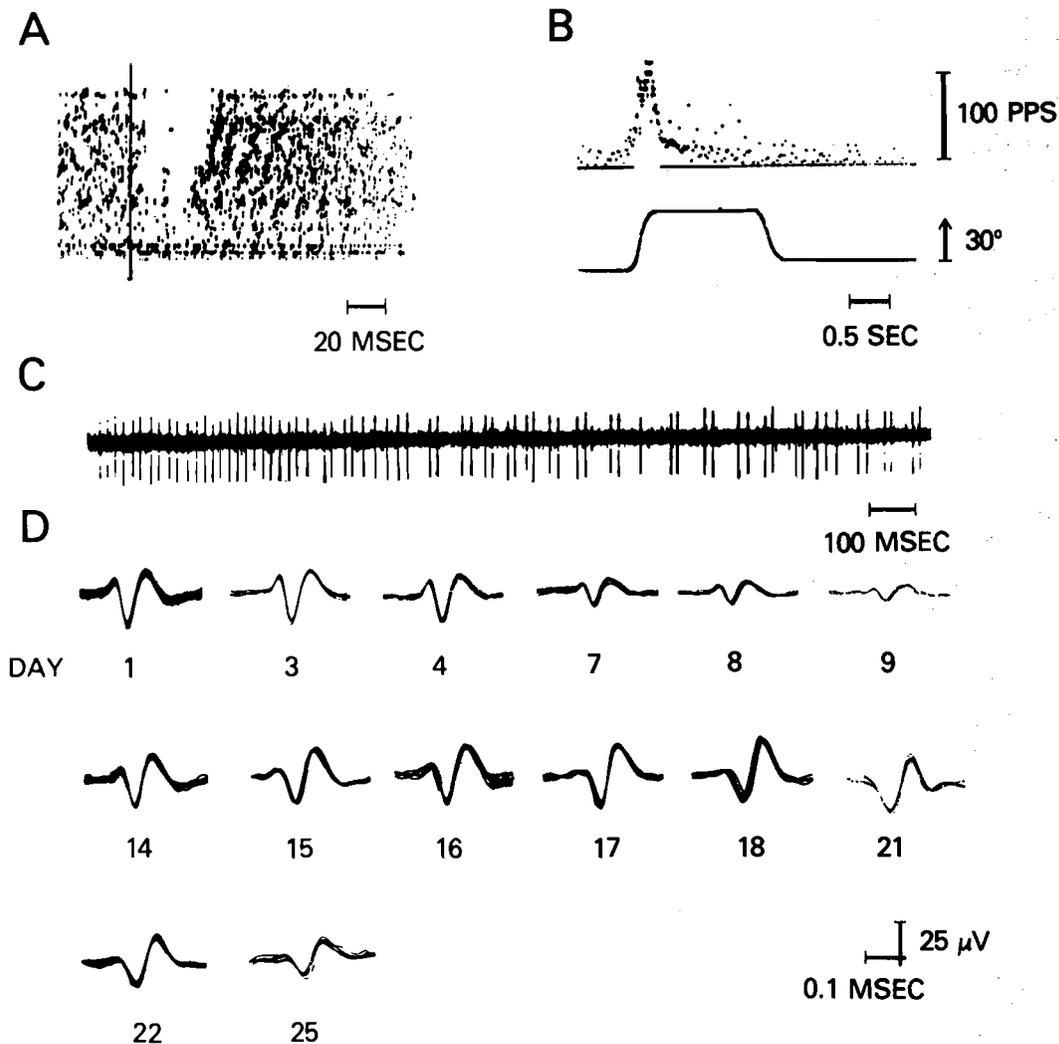


FIG. 1. Identification of the spindle primary TX7A15 from gluteus minimus muscle. *A*: dot raster of spontaneous activity during constant stretch of the muscle showing the inhibitory effect of progressively increased amplitude muscle twitches (at vertical line, increasing amplitude each row upward). *B*: afferent firing frequency in response to a manually delivered external rotation of the femur. Lower trace indicates output of a hand-held goniometer moved in parallel with the limb; arrow in calibration indicates movement causing stretch of the muscle. *C*: spontaneous activity during ketamine anesthesia, limb in neutral position. Paired firing pattern was distinctive for this unit. *D*: multiple tracings of the discriminated unit at various days during the period it was recorded, showing some waxing and waning of the signal amplitude but generally constant waveform. Day to day identification was based on location, conduction velocity, and twitch sensitivity.

tion of rapidly modulated rates and the possible duration of postsynaptic effects.

UNIT CHARACTERIZATION. Ketamine anesthesia (100 mg sc for a 3.5- to 4.5-kg cat) was used during the unit characterization because it preserved muscle tone and apparent gamma-motoneuron bias to spindles, which were frequently spontaneously active at physiological limb positions (see Fig. 1C).

Manual manipulation usually established the probable muscle or muscle group of origin of a

proprioceptor. Using either the implanted length gauges (if appropriate) or a hand-held electronic goniometer, a crude estimate of dynamic index was obtained by manually applied ramp-and-hold stretches, with instantaneous spike frequency and presumed muscle length displayed on a storage scope (Fig. 1B).

The point of maximal vibratory sensitivity on the muscle belly and tendons was established with a hand-held probe (100 Hz) and the maximum frequency of entrained responses deter-

mined. If the muscle was not already fitted with implanted electrodes, a pair of insulated needle electrodes was inserted percutaneously into the muscle near the presumed spindle location. With the muscle stretched and the proprioceptor steadily firing, increasing amplitude single electrical stimuli were delivered to the muscle and a raster display generated showing the pause in activity caused by local twitch unloading of the spindle (see Fig. 1A). Golgi tendon organs were activated rather than silenced by such stimulation, and incorrect muscle locations required unusually large amplitude twitches to unload a spindle actually located in an adjacent muscle.

It was usually possible to excite the spindle afferent directly in the muscle as the electrical stimulation amplitude was increased. The latency

of such responses was obtained at faster sweep speeds using the unprocessed microelectrode signal to confirm the shape and all-or-none properties of the DRG action potential. The site of electrical stimulation was recorded and the nerve conduction distance was determined for each unit during a postmortem dissection of the limb. Because of the uncertainties regarding the exact site of impulse initiation with these stimuli, we estimate 5–20% uncertainty in the conduction velocities given in Table 1 with smaller errors for more distal muscles.

All of the above data were photographed from the face of the storage oscilloscope using Polaroid film to obtain a record for reference in subsequent sessions and unit reidentification.

In two cats, the electrode signals were tape

TABLE 1. *Muscle spindle afferents chronically recorded and identified*

Identification No.	DRG	Muscle Origin	Conduction Velocity	Fig. No.	Vibration, Hz
<i>Primaries</i>					
LX4A	L ₇	Gluteus maximus	89		>210
NX2A	L ₇	Peroneus tertius			>300*
NX3A	L ₇	Tibialis anterior		5, 6	*
NX5A	L ₇	Flexor digitorum longus			*
OX5B2	L ₇	Extensor digitorum longus			215
OX6A4	L ₇	Gemellus inferior	70		230
QX5B	L ₇	Extensor digitorum longus			*
SY9B1	S ₁	Posterior biceps	105	2	175
SX10A1	L ₇	Peroneus tertius	94		325
TX3A3	L ₇	Second interosseus	97		320
TX3A11	L ₇	Triceps surae	79		380
TX4A2	L ₇	Extensor digitorum longus	92		200
TX4A7	L ₇	Extensor digitorum longus	85	8	300
TX4C7	L ₇	Adductor femoris			450
TX4B4	L ₇	Plantaris			>300
TX6A2	L ₇	Popliteus	91		260
TX6A8	L ₇	Extensor digitorum longus	83	8	400
TX6A7	L ₇	Quadriceps femoris			360
TX7A15	L ₇	Gluteus minimus	90	1, 9	450
TX8B9	L ₇	Peroneus longus	109	5, 6, 7	210
TY10A24	S ₁	Posterior biceps		2	480
<i>Secondaries</i>					
OX1B1	L ₇	Semitendinosus	17		
QX5A	L ₇	Interosseus			†
SX3B2	L ₇	Adductor digitorum secundi medius	57		190
SX3A4	L ₇	Posterior biceps	43	2	NS
SX10A5	L ₇	Extensor digitorum brevis	50		NS
RX7A3	L ₇	Flexor hallucis longus	56		NS
TX1A3	L ₇	Medial gastrocnemius	26		200
TY2A2	S ₁	Medial gastrocnemius	22	3, 4, 7	290
TY2A14	S ₁	Medial gastrocnemius	47		450
TX3B3	L ₇	Flexor digitorum brevis	85		220
TX4A9	L ₇	Flexor digitorum longus	56		270
TX4A11	L ₇	Gluteus	36		360
TY10B14	S ₁	Anterior biceps	31		220

NS, not sensitive to vibration. * Responsive to low dose succinylcholine. † Not responsive to succinylcholine.

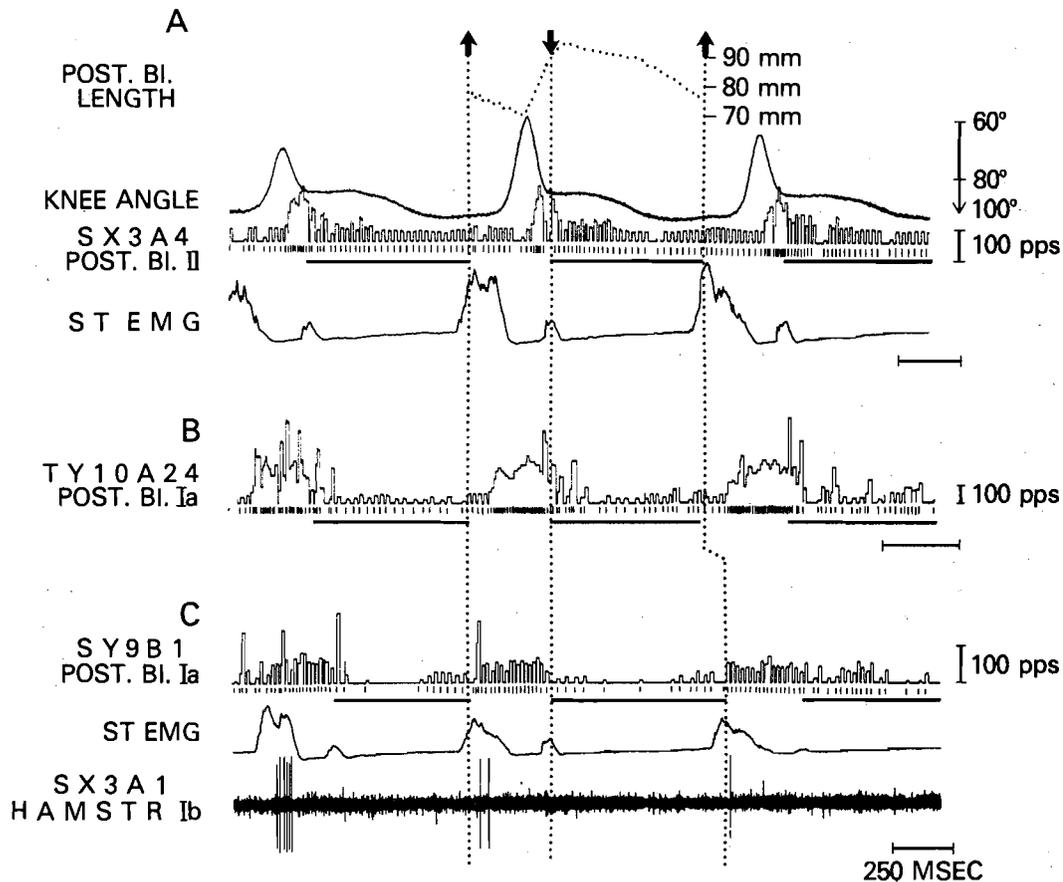


FIG. 2. Activity of proprioceptors from the hamstring muscles during normal walking; vertical dotted lines indicate footfall (downward arrow) and footlift (upward arrow) for videotape-analyzed step cycles. *A*: from top down, length of posterior biceps muscle (from videotape stills), knee angle (from implanted length gauge, muscle stretch in direction of arrow), activity of posterior biceps and individual discriminator acceptance pulses, heavy horizontal bars showing stance phases of step cycles (foot on treadmill in videotape stills), and rectified and integrated EMG activity from semitendinosus muscle. *B*: activity of a posterior biceps spindle primary in another cat walking at the same speed. *C*: activity of a posterior biceps spindle primary (same cat as *A* but different day); bottom trace shows actual signal from another microelectrode with simultaneous activity later determined to be arising from a hamstring muscle Golgi tendon organ.

recorded during the administration of low-dose intravenous succinylcholine (0.2 mg/kg), a procedure reported to distinguish reliably between spindle primary and secondary endings (14). This observation was confirmed, but both animals succumbed to respiratory depression (a synergistic action with ketamine was suspected), and the procedure was subsequently omitted.

RESULTS

Table 1 summarizes data for the 34 spindle afferents recorded and identified. The prefix letters of the identification code indicate the cat number. Separation into primary and secondary endings was based primarily on conduction velocity, with consideration of

other data as available (see footnotes) for cases where conduction velocity was not conclusive (65-85 m/s) (27) or unobtainable. Conduction velocity and succinylcholine responses were the clearest discriminators of ending type (the latter evaluated in only two animals because of technical difficulties). The response to vibration (Table 1, last column) was occasionally helpful, but by no means reliably distinctive for separation of primaries and secondaries. As discussed later and in agreement with recent reports (9, 21, 23), pure velocity sensitivity (e.g., as manifested by dynamic index) was neither a clearly distinguishing feature of spindle primary endings nor a discernible influence on

their activity under conditions of normal fusimotor tone and physiological length changes.

Hamstring muscle group

The activity of different kinds of afferents from the hamstring muscle group was recorded and their activity during three step cycles for each is compared in Fig. 2. The hamstrings are both knee flexors and hip extensors, and their length is, therefore, not simply determined by the knee angle as obtained from an implanted length gauge across the knee (Fig. 2A). An accurate estimate of the length changes of this muscle group was possible by measuring from video stills the distance between the tuberosity of the ischium and the muscle insertion point on the tibial crest (one-third of the way down the tibia). In agreement with Peters and Rick (30), it was found that the hamstrings shorten by about 5 mm during the flexion phase (F phase) and then are quickly stretched by approximately 20 mm during the first extension phase (E1) prior to footfall (Fig. 2A). During stance, the hamstrings shorten passively.

The EMG of posterior biceps was not available but is it likely that it closely followed the recorded EMG of the synergistic semitendinosus (11). The maximal burst of activity in these muscles starts just prior to foot lift and ends before the knee reaches maximum flexion. Since the hamstrings shorten slightly during this activity period, one would expect spindle activity from these muscles to slightly decrease due to receptor unloading, unless the latter is prevented by concomitant gamma motor activity. The spindle afferents in the present sample differed greatly in this respect. The posterior biceps secondary ending (Fig. 2A) showed only a small possible gamma static bias during the flexion phase (just after foot lift) and fired mainly during and in proportion to the passive stretch during the first extension phase (a "passive" firing pattern in the nomenclature of Prochazka et al. (31, 32)). On the other hand, the primary endings (represented in Fig. 2B and C) showed considerable activity during the same active shortening period (an active firing pattern) for stepping movements, which were quite similar as seen on videotape. The time course and amplitude of hamstring muscle length for

Fig. 2C (same cat as Fig. 2A) included a 3-mm shortening during the flexion phase and a 16-mm lengthening during the E1 phase for the step cycle between the vertical dotted lines. It seems necessary to hypothesize a major fusimotor driving of the spindle primaries during the F phase, and to conclude that such influence was absent or greatly diminished for the spindle secondary ending. However, the time course of such fusimotor driving during swing would have had to be somewhat different for the two posterior biceps primaries and not well correlated with the timing details of the normal "two-burst" hamstring EMG.

Both spindle primaries and secondaries behaved quite differently from Golgi tendon organs (GTO) in this and other muscle groups. Figure 2C compares the activity of a hamstring GTO afferent (*SX3A1*) recorded simultaneously with the hamstring spindle primary (*SY9B1*) but on a different electrode. During passive manipulation, this GTO unit responded only phasically when the knee was held in extreme extension, particularly when this elicited an active withdrawal by the cat. During walking, this same unit fired consistently with a latency of approximately 80 ms following the onset of EMG (from semitendinosus). Passive stretch of the muscle during walking was not an effective stimulus for this or other GTOs from our data.

Ankle extensor muscles

The firing pattern of triceps surae primary spindle endings during walking has been described by Prochazka et al. (31, 32), but nothing is known about the firing patterns of triceps surae secondaries under the same conditions. In our experiments, recordings were made from three medial gastrocnemius (MG) secondaries, although reliable unit separations were obtainable during walking for only one. Its activity during walking is shown in Fig. 3A along with the output of the ankle length gauge and the MG EMG. As for the posterior biceps secondary ending (Fig. 2A), the MG secondary activity also reflects closely the parent muscle length (predominantly determined by ankle joint angle during walking). The firing pattern seemed relatively independent of the recorded extrafusal EMG activity or small variations in the EMG among step cycles,

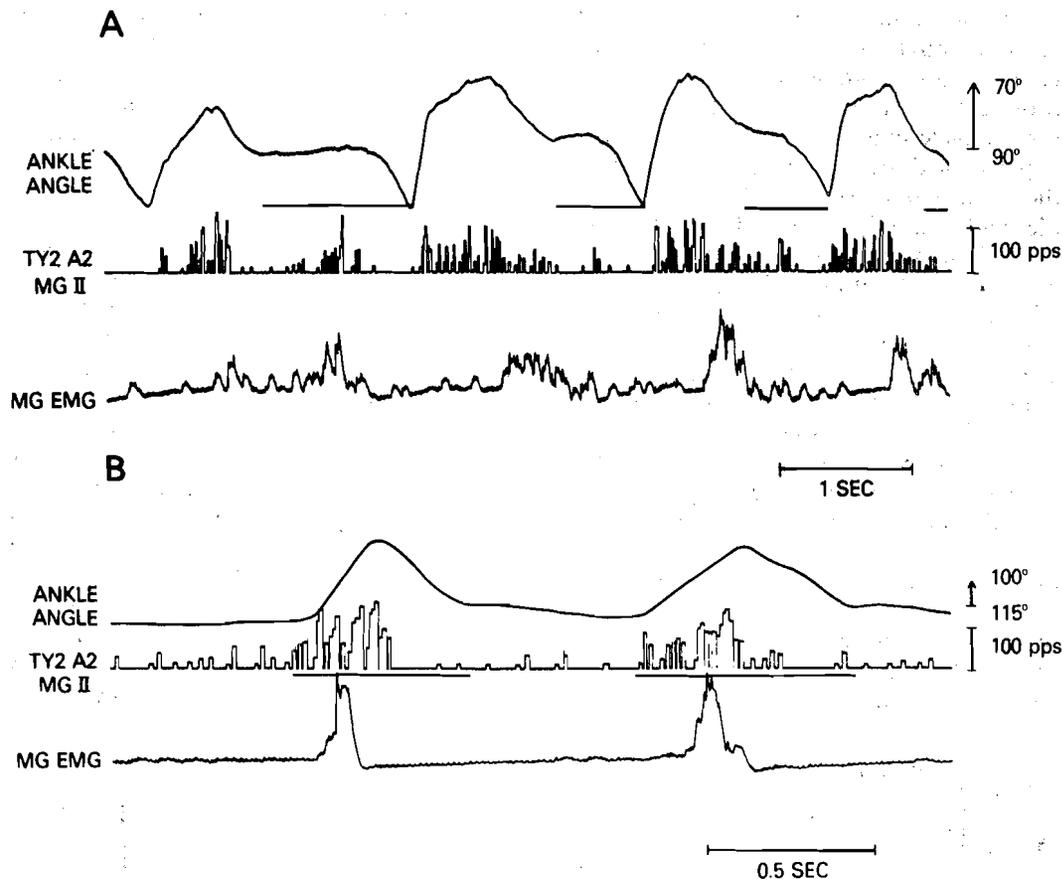


FIG. 3. Activity of a spindle secondary afferent from medial gastrocnemius muscle. A: during walking; ankle angle from implanted length gauge, muscle stretch in direction of calibration arrow; horizontal bars show stance phase; unit activity shown as instantaneous frequency; EMG rectified and integrated. (These records obtained 2 days postoperatively, with unsteady gait apparent from slow swing phases.) B: animal held over still surface, manually lowered until beginning to support weight (horizontal bars indicate foot down).

and might be characterized as predominantly "passive."

Figure 3B shows the same secondary ending under different conditions. Here the cat was manually held above a nonmoving surface and gently lowered to where his dangling hindlegs touched the surface and began to support his weight, then raised again off his feet. Just prior to each footfall (at arrows), there was buildup of irregular, low-frequency spontaneous activity. The spindle began firing very vigorously within 50 ms of foot contact, when the passive stretch of the MG muscle at the ankle had just begun, and it fired at rates in excess of 100 pulses/s during the time when the MG muscle was electrically active (although no change in overall muscle stretch was effected). There was abrupt cessation of spindle firing as the mus-

cle slowly (and passively) shortened during the lift off the surface. During walking, this secondary ending fired faster than 50 pulses/s only when ankle dorsiflexion exceeded 100°. During these manipulations, the spindle fired at 50–100 pulses/s for 115° ankle angles while the knee was held flexed, further shortening this muscle. Although the spindle secondary afferent was still active only when being stretched, the magnitude and time course of its activity suggests a strong fusimotor influence (presumably static), which was abruptly withdrawn as the ankle extended. The possibility that fusimotor activity (possibly dynamic) caused an increase in velocity sensitivity of this secondary cannot be excluded. Such action has been reported during acute studies of some spindle secondaries in cat soleus muscle (10).

Fusimotor influence on spindle secondaries is thought to be predominantly via the gamma static motoneurons, which produce propagated fast twitches in intrafusal chain-type muscle fibers, which are known to be capable of directly driving the afferents in the absence of muscle lengthening (1). Struppler and Velho (38) reported that skin stimulation in humans was a powerful inducer of group II spindle afferent firing in the absence of muscle stretch. In the present experiments, skin stimulation was applied through a bipolar pair of electrodes implanted subcutaneously at the back of the ankle (sural nerve distribution). As seen in Fig. 4, a 100-ms train of 6 pulses evoked a flexor reflex in the hindlimb at a time when the cat had just placed his foot on the nonmoving treadmill. Following the reflex flexion, there was a second extension and placement accompanied by substantially more MG EMG activity than in the first placement. Although the final joint angles for the two extensions were similar, only the second was accompanied

by MG spindle secondary activity. This activity pattern would be consistent with an "active" response to alpha-gamma coactivation, but was seen only following the cutaneously evoked reflex and not during normal walking.

Ankle flexor muscles

Although spindle primary endings from ankle extensor muscles were studied by Prochazka et al. (31, 32), little is known of their counterparts in the non-weight-bearing antagonists, the ankle flexors. Studies by Perret and Berthoz (29) in decorticate cats with rhythmic "locomotor" activity indicated that both ankle flexors and extensors obeyed the principle of alpha-gamma coactivation, but that the two muscle groups differed as to type of gamma activation. The authors concluded that the "static action is important and possibly occluded the dynamic one in flexors, whereas a strong dynamic action occurs in extensors in addition to a weak static effect." A stronger static

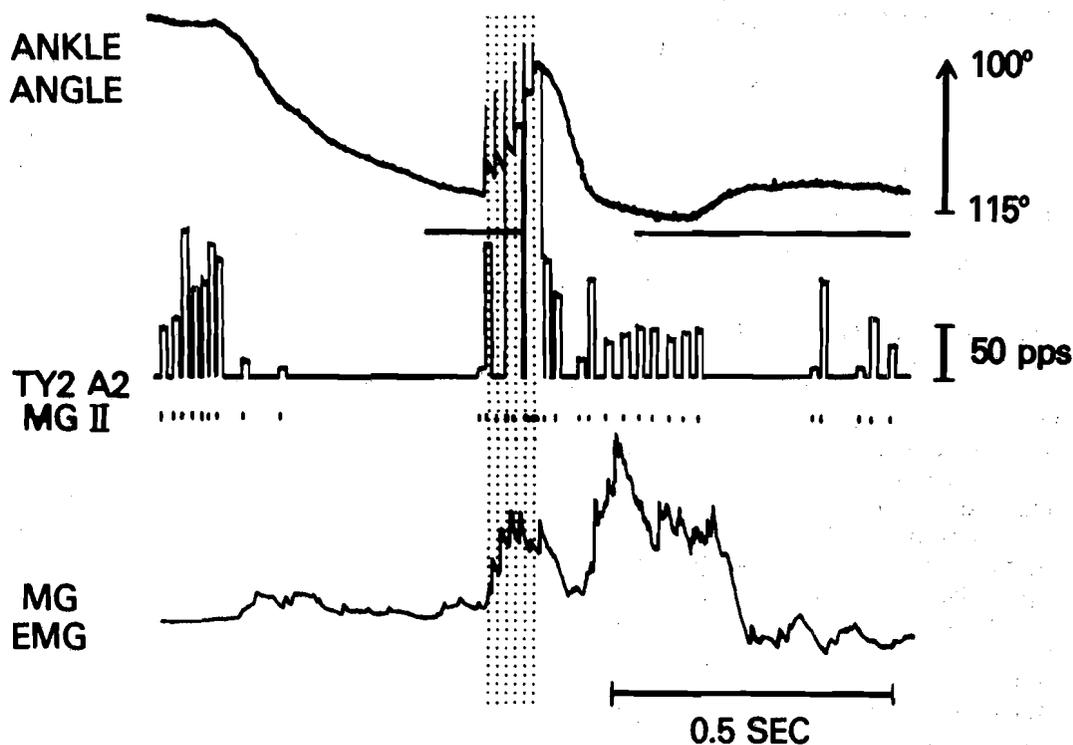


FIG. 4. Effect of electrical stimulation train (dotted area) delivered to skin at the back of the ankle just after the animal set its foot down in a slow movement. The foot was rapidly lifted and then replaced on the ground with increased spindle secondary activity and extrafusal activity during the second stance (medial gastrocnemius muscle, EMG rectified and integrated).

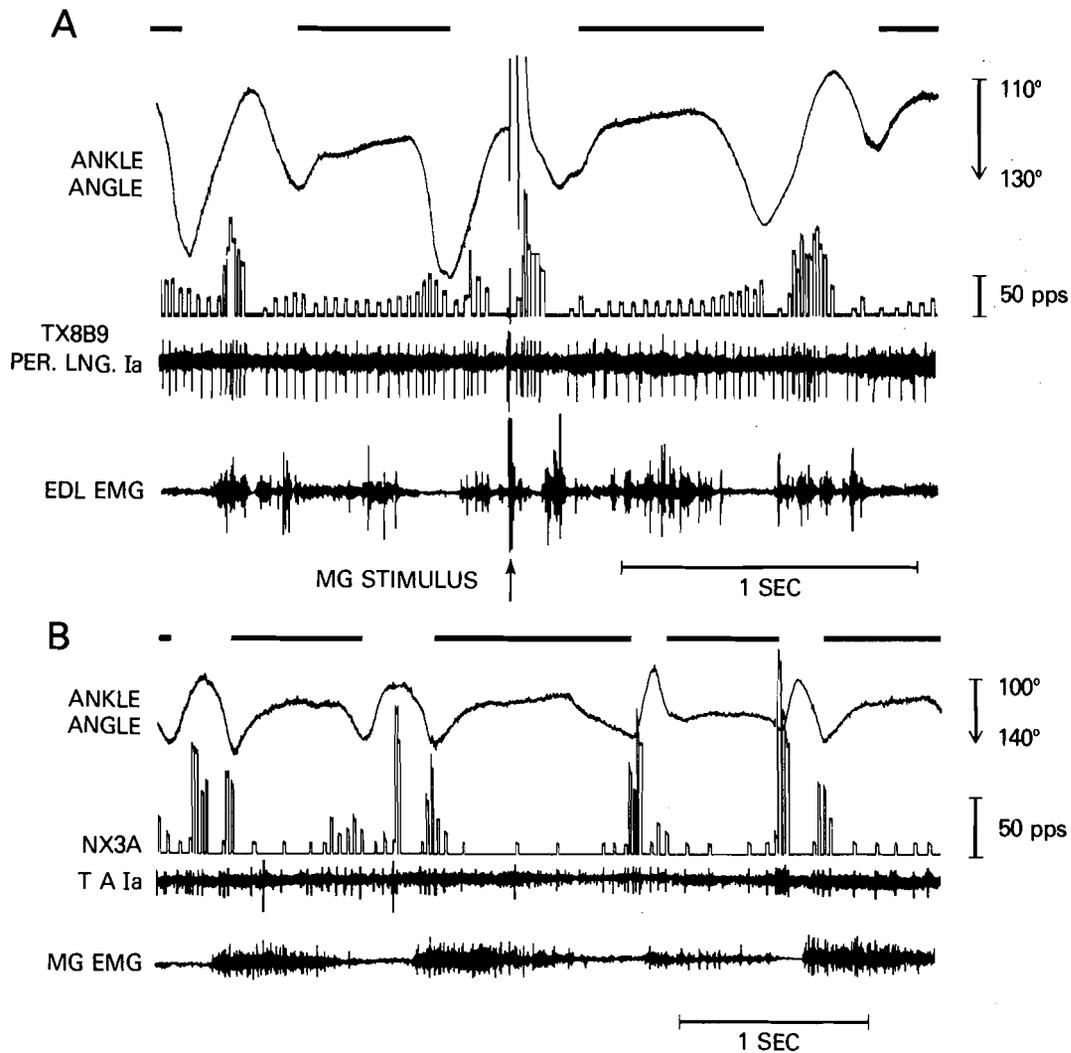


FIG. 5. Activity of ankle flexor spindle primaries during walking. *A*: three step cycles showing activity from an afferent in peroneus longus muscle and unprocessed EMG activity in extensor digitorum longus (EDL) muscle; single electrical stimulus delivered to medial gastrocnemius muscle at midswing of second step cycle (arrow) results in second swing-phase burst of the spindle primary without altering ankle trajectory (confirmed on videotape, gauge signal obscured by shock artifact). *B*: four step cycles showing tibialis anterior afferent activity, which increased and became phase advanced as gait speed increased (last two step cycles).

action on ankle flexors was suggested by their observation that there was virtually no pause in spindle firing during the periods of flexor contractions, whereas such pauses were much more prominent in ankle extensor spindle primaries.

Two pure ankle flexor spindle primaries were recorded in the present study and both had their peak activity (without pause) during the active shortening of their respective muscles. Figure 5A shows the activity of a primary ending from peroneus longus, which

runs from the lateral surface of the fibular head to the lateral metatarsals. During walking, the unit was maximally active during the period of ankle flexion (F phase) when the ankle flexors actively shorten (19): there is only a suggestion of a pause at the point of maximal shortening rate in the third step cycle. Passive stretch activation of the spindle was modest at the end of stance (50 pulses/s at 130° ankle extension) and virtually absent for the lesser extension in E1 (110–120°). Thus, during normal stepping

(first and third step cycles of Fig. 5A), the spindle primary was dominated by alpha-gamma coactivation, presumably through static fusimotor efferents.

In the second step cycle of Fig. 5A, we were able to change the normal insensitivity to passive stretch by delivering a single 1-ms electrical pulse to the MG (antagonist) muscle just at the end of the flexion phase. This stimulus was too weak to evoke a significant MG contraction or to lead to increased ankle extension during E1. Analysis of video records revealed that the ankle extended at a rate of 149°/s in the extension following the MG stimulus (length gauge trace obscured by stimulus artifact) while the ankle extension during E1 of the preceding step cycle was at 165°/s. Hence, the burst of spindle firing following the MG stimulus with a 50-ms latency was not due to increased muscle stretch, but appears to have been related to a reflexly induced fusimotor enhancement of this spindle ending's stretch sensitivity. The mechanism of this reflex gamma activation is unclear, but must have been related to the antidromic activation of Renshaw cells and/or the orthodromic activation of muscle receptors within MG. Whether or not there was a coactivated alpha-motoneuron burst is uncertain (no significant change is apparent in the EMG activity recorded from extensor digitorum longus, a toe extensor and ankle dorsiflexor).

The behavioral response to the stimulation is also of interest. The ankle extension following MG stimulation led to a delayed placing of the foot, which was held in the air for 75 ms at the end of the E1 extension and then slowly placed on the treadmill. During this delay, the extensor digitorum longus (EDL) muscle showed a much longer burst than that usually seen just preceding footfall. It is possible that the preceding burst of ankle flexor spindle activity induced by the electrical stimulation was contributing to this increased activity of EDL, also an ankle flexor. Similar "hesitations" preceding foot placing have been seen in chronic spinal cats (15), suggesting that final foot placement is relatively independent of preceding E1 extension at the ankle.

The other ankle flexor spindle primary, from tibialis anterior, resembled the peroneus longus afferent in most respects. The peak firing occurred during the period of active ankle flexion (without pause), pre-

sumably as a result of alpha-gamma coactivation (Fig. 5B). Activity related to passive stretch was seen at the end of stance and, additionally, during the E1 stretch. Although both stretches here (E3 and E1) had similar final angles, this spindle responded much more vigorously to the latter, suggesting the possibility of residual effects from slowly relaxing intrafusal contractions initiated in flexion phase.

The timing of the peak active response during flexion was usually constant when the gait was stable, but changes in gait pattern could be reflected by shifts in the timing of this firing. When the animal accelerated in the last two step cycles of Fig. 5B, this peak appeared shifted to before the start of the actual flexion movement. Since no tibialis anterior EMG was available, it is unclear whether this phase shift occurred for both the alpha- and gamma-motoneurons, but such phase advances have been described in some muscles with increasing gait speed (11). Figure 5B illustrates a danger in interpreting spindle activity as either active or passive. An examination of only the last two step cycles might lead one to ascribe the end stance activity to passive stretch sensitivity alone. However, allowing some license on precise timing, the ankle flexor data seem best summarized as good examples of an alpha-gamma coactivation pattern consistent with the strong static fusimotor input proposed.

This pattern appeared to be retained during nonlocomotory movements as well. For the same two ankle flexor spindles, activity during voluntary lifting of the foot while standing quietly (Fig. 6) suggests a static fusimotor activation during and possibly preceding the active flexion. However, both spindles paused during the maximal rate of muscle shortening, although these rates were no greater than occurred during walking when little or no pause was seen.

Alpha-gamma coactivation was also apparent during more rapid and ballistic movements. We examined the response of spindle endings to rapid paw shakes (10 Hz) evoked by stimulation of the skin around the ankle (100-ms train of 6 pulses). Figure 7 shows such a stimulus given just before the swing phase, which resulted in a two-cycle shake superimposed on the flexion phase of walking. Short bursts of activity in the ankle flex-

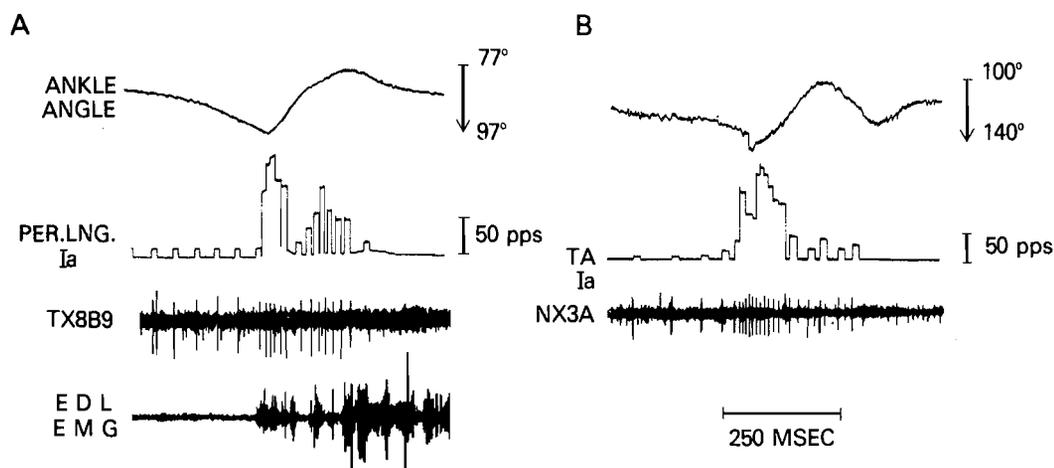


FIG. 6. Ankle flexor spindle primary activity during small postural adjustments, parent muscles stretched for joint angle deflections in direction of calibration arrows. *A*: peroneus longus primary afferent during muscle shortening. EMG from the synergistic extensor digitorum longus (EDL) muscle is included for reference. *B*: tibialis anterior primary afferent activity during muscle shortening.

ors were immediately followed by high-amplitude EMG bursts in the ankle extensors. This extensor contraction decelerated and reversed the ankle flexion after the expected delay of approximately 50 ms from the EMG onset. Simultaneous recording from two spindle afferents, an ankle flexor primary (peroneus longus) and an ankle extensor secondary (MG) on different electrodes, showed that peak spindle activity coincided with peak EMG activity of each parent muscle. For the MG secondary, the EMG peaks occurred when the ankle was flexing (the knee was held relatively constant) and the muscle was stretched. However, another brief interspike-interval peak occurred during each of the subsequent ankle extensions (see arrows in stippled areas) when the muscle was actively shortening (ankle and knee). Similarly, the peroneus longus primary had two peaks of activity in each shake cycle, one related to passive muscle stretch (EMG from the synergist EDL was present but contraction force would not yet have developed) and another during subsequent active muscle shortening (arrow). The spindle activity during muscle active contraction and shortening consisted of only one or two "extra" spikes, but it consistently indicated intrafusal contractions, which were either nearly as rapid as the extrafusal ones or which were initiated by gamma-motoneuron firing leading the alpha-motoneurons. In either case, these records indicate that

fusimotor activity can be rapidly modulated and can, in turn, rapidly modulate spindle activity despite slow twitch contraction times generally ascribed to intrafusal muscle fibers (6). This conclusion differs from the conclusions drawn by Prochazka et al. (32) from their recordings of triceps surae primaries during paw shaking. These authors found little indication of fusimotor activity except for possible gamma dynamic influence, which was not apparently modulatable at these frequencies. Our data shows no evidence for gamma dynamic influence on ankle flexor primary endings and, furthermore, suggests gamma static coactivation of spindles with each extrafusal contraction in both flexors and extensors. It should be noted that we have no comparable data from triceps surae primary endings and that our shake reflex was induced in the middle of a step cycle. On the other hand, our data completely support the finding of Hagbarth et al. (20) that the gamma system participated phasically in rapid alternating contractions during voluntary movements in humans (approximately 3–4 Hz).

Toe muscles

A considerable number of the afferents in the present study were derived from toe muscles. Activity in toe flexor primaries (plantaris, flexor digitorum longus, and flexor hallucis longus, which are physiolog-

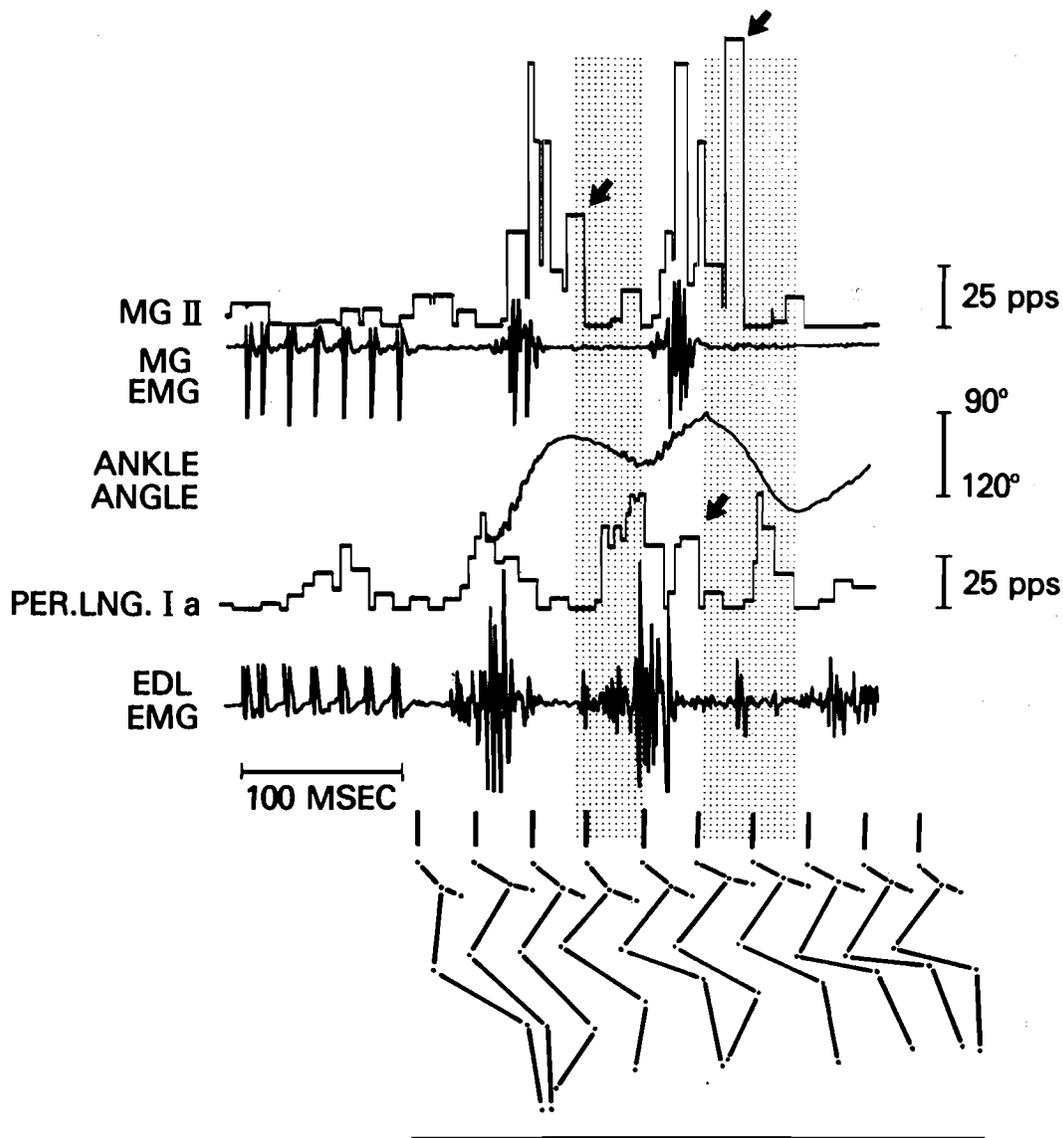


FIG. 7. Spindle activity during a brief shake reflex elicited during swing phase of walking gait by 100-ms train of electrical stimulation pulses to posterior ankle skin (at time bar); dotted areas indicate periods of ankle movement in plantar extension direction, shortening the medial gastrocnemius from which a spindle secondary was recorded, and stretching the peroneus longus muscle from which a spindle primary was simultaneously recorded. Arrows indicate spindle activity out of phase with parent muscle stretch and which may represent short-latency effects of fusimotor activity accompanying the extrafusal activity, which leads the movements by approximately 50 ms (medial gastrocnemius and extensor digitorum longus EMG activity unfiltered). Stick figures at bottom were traced from every second video field; dots indicate position of reflective markers on bony landmarks (see METHODS).

ically extensor muscles) was similar to that described by Prochazka et al. (31, 32) during walking. The toe flexor spindles were all relatively quiet during the swing phase but, in all cases, responded with a burst of activity to toe dorsiflexion at footfall.

During stance, these units had variable amounts of activity. One spindle (flexor digitorum longus) showed a marked burst of activity at the end of stance (up to 250 pulses/s). A somewhat smaller late stance response was reported by Prochazka et al.

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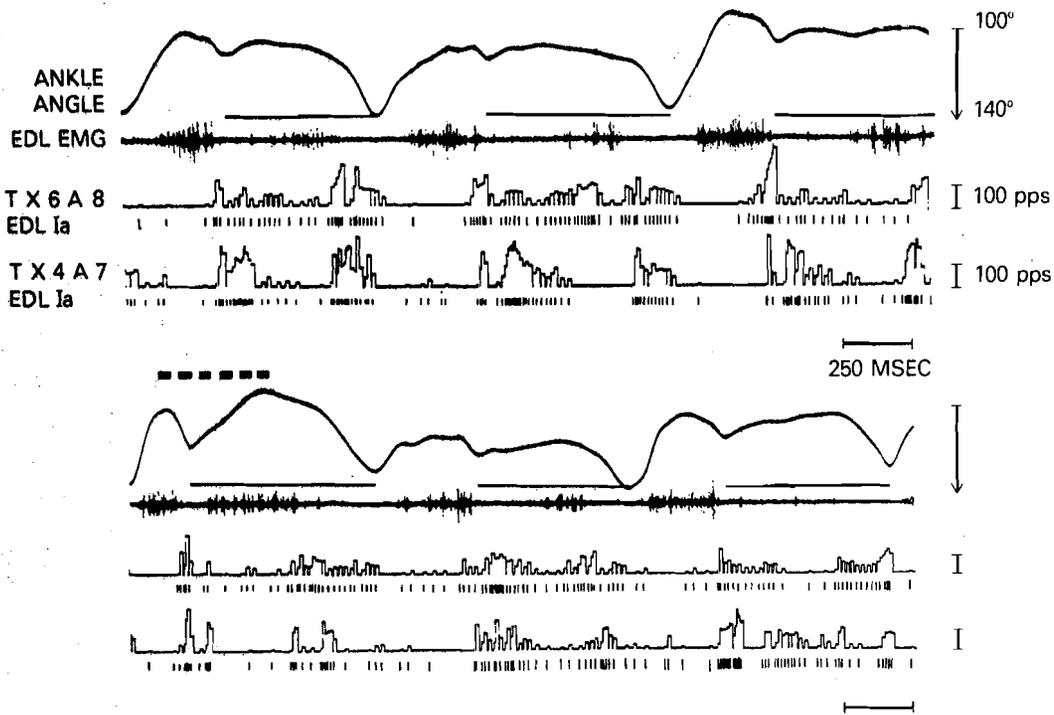


FIG. 8. Activity of two simultaneously recorded extensor digitorum longus spindle primaries during normal (top group) and perturbed (bottom group) locomotion. From top, ankle angle from implanted gauge (downward deflection stretches EDL muscle), horizontal bars indicating stance phase for ipsilateral foot, unfiltered EMG from implanted EDL bipolar electrodes, spindle activity shown as instantaneous firing rate and individual discriminator acceptance pulses for both afferents. Note prominent peak of activity in unit TX4A7 (bottom trace) just after footfall, which is essentially absent for TX6A8. Heavy dotted line in bottom group indicates manual thrust downward on back, resulting in a large, rapid E1 phase followed by an exaggerated yield phase with abnormal EMG activity in EDL and decreased spindle activity.

(32) for plantaris muscle primary endings. During this phase these muscles undergo a lengthening contraction, which presumably combines both active and passive stimuli to the toe flexor spindle endings.

Activity in the antagonist muscle, extensor digitorum longus (EDL), has not been described previously and revealed unusual features in the four primary endings that we identified. Two were obtained from the same electrode on different days (TX4A2 and TX4A7) and two of the four were recorded simultaneously from different electrodes (TX6A8 and TX4A7). Figure 8 shows two simultaneous records along with unfiltered EMG from bipolar electrodes implanted in EDL. The EDL muscle is most active during the swing phase, particularly E1, but we typically observed some more variable activity during late stance. Its length changes during the step cycle have been

studied in detail by Goslow et al. (16). During the swing phase, the changes are small since the action of ankle flexion is counteracted by digit plantar flexion for the F phase and ankle extension tends to be counteracted by active digit dorsiflexion during E1. Both spindle primaries were virtually silent during the entire swing, indicating an absence of static fusimotor coactivation with the near-isometric extrafusal contraction. Both spindles did begin firing vigorously just before foot placement. This may be related to ankle extension outweighing digit dorsiflexion and/or gradual accumulation of slow fusimotor contractions accompanying the preceding extrafusal activity. Both spindles responded to the passive stretch of EDL at the end of stance.

An unexplained difference between the two spindles was noted during the period just after footfall. At this point the muscle

was always electrically silent and would have been shortening passively as a result of dorsal yielding at both the ankle and toes (there is a small moment about the knee, but the change in angle is small and distal shortening should have dominated). The spindle TX4A7 had a consistent and significant burst of activity just after footfall, which was virtually absent for the other simultaneously recorded EDL Ia. During the first step cycle in the lower trace of Fig. 8, a brief manual thrust was applied to the back of the animal, a maneuver which Prochazka et al. (32) reported greatly increased both extrafusal EMG and spindle activity and presumed gamma bias in triceps surae. In response to this push, our cat made an accelerated E1 ankle extension (apparently accounting for the high firing rate of both spindles as compared to late E1 responses in the subsequent step cycles). The push was maintained during early stance phase, causing the animal to respond with an exaggerated yield (see ankle angle trace) and an unusual and sustained EDL contraction during which both spindles were even more inactive than usual. Any possible alpha-gamma coactivation of EDL was, at most, too weak to overcome the spindle unloading caused by EDL shortening during this yield.

The two other EDL primaries showed essentially the same main features in their activity, leading us to conclude that EDL receives very little alpha-gamma coactivation during walking, even when perturbed. This is somewhat surprising in view of the very strong alpha-gamma coactivation seen in pure ankle flexor muscles (above). In addition, some but not all EDL spindles appear to receive strong fusimotor stimulation in the absence of extrafusal activity.

Hip-stabilizing muscles

Several spindles were recorded from hip muscles (e.g., gluteus, gemellus), which could not easily fit into a classification of flexors and extensors. Nevertheless, these units fired reproducibly at certain points of each step cycle. The spindle primary in gemellus inferior (a thigh abductor) was exquisitely sensitive and was activated by respiratory movements when the animal was anesthetized (ketamine). During walking this unit fired a 100 ms duration burst at 240 pulses/s after footfall and a similar burst

just before foot lift. Uncertainties regarding the mechanics and function of such muscles make interpretations difficult and call for more detailed kinesiological information than can be obtained from videotape.

A more detailed study was possible for a spindle primary identified as originating in gluteus minimus muscle. On manipulation, this spindle was maximally excited by external rotation and extreme extension of the hip, both of which stretch the muscle. A length gauge was implanted along the course of the muscle from its origin on the anterior iliac crest to its insertion on the greater trochanter of the femur. A bipolar EMG electrode pair was implanted in the belly of the muscle (taking care to avoid the spindle location as determined by the area of maximal vibratory sensitivity). As this spindle continued to generate clear unit recordings for 18 days after the minor surgical procedure (see Fig. 1), it was possible to obtain detailed records of its activity under essentially normal conditions.

The gluteus minimus muscle typically produced three variable bursts of EMG activity during the stance phase and was electrically silent during most of the swing phase (Fig. 9A). The length changes of the muscle were similarly variable, with most lengthening occurring during stance (when active) and shortening during swing (when silent). The main burst of activity in the gluteus minimus primary occurred during the swing phase when the EMG was silent and the muscle was shortening passively. The onset of this main burst preceded both the length change and the EMG silencing. This paradoxical pattern is seen even more clearly in Fig. 9C where the animal was not walking but was making postural adjustment movements, which required strong activation of the gluteus minimus muscle. Under these circumstances the interspike interval of the spindle firing was closely but inversely correlated with the integrated EMG record. In contrast, the spindle activity seemed relatively independent of the overall muscle length changes as reflected in the length gauge, with large bursts of activity occurring when the muscle was actually shortening and no apparent response to lengthening. This latter is understandable in view of observations during postmortem dissection and simulation of hindlimb walking move-

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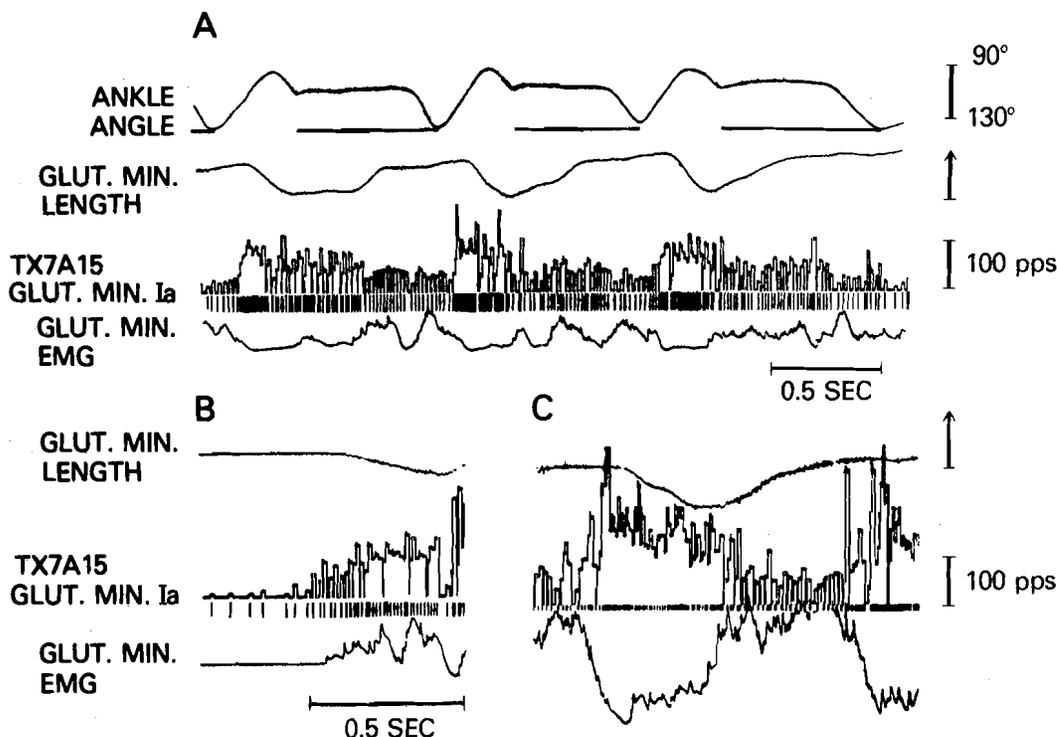


FIG. 9. Activity of a gluteus minimus spindle primary and correlation with parent muscle length (from implanted gauge, upward deflection indicates stretch) and EMG (implanted bipolar electrode, rectified and integrated). A: during walking, with ankle angles and stance times for reference, note tendency for muscle shortening to occur in absence of EMG and for EMG to occur during muscle stretch; spindle activity occurs mostly when muscle is shortening passively. B: during small postural movement (animal sitting), showing spindle activity increasing during an active contraction of the muscle. C: during larger postural adjustment, showing spindle activity inversely correlated with EMG activity and little influence from muscle length.

ments, which revealed that the normal muscle length changes constitute only a small percentage of the total muscle rest length.

The reciprocal relation between the EMG and the spindle firing may be of more importance. It is possible that the spindle may have been under continuous fusimotor activation, but was situated so as to be readily unloaded by extrafusal contractions not reflected in overall muscle length. Alternatively, the gamma-motoneurons influencing this spindle may have been activated out of phase with the alpha-motoneurons. However, the spindle activity in Fig. 9B is best described as resulting from a simple alpha-gamma coactivation. The animal was making a small postural adjustment while standing quietly, and the spindle is seen to begin firing just before the movement (in fact, slightly before the parent muscle EMG), just as was seen for ankle flexors in Fig. 6. However, even here, a larger burst of spindle activity

occurs after the gluteus minimus muscle completes its active contraction and becomes electrically silent (end of trace in Fig. 9B).

DISCUSSION

There is a growing body of observations of spindle afferent activity during some form of movement initiated by the experimental animal, as opposed to movements externally applied by the investigator. It has been the practice to attempt to infer patterns of fusimotor activity from those aspects of spindle discharge that are not accountable by the properties of deafferented passive spindles. The inferred gamma-motoneuron activity is then temporally related to the alpha-motoneuron activity (as determined from EMG records), and this relationship analyzed in terms of its support for length-servo models of motor control such as Merton's (28) "fol-

low-up" servo. This analysis has led to strikingly different conclusions depending on the quite disparate sources of data. While Merton's prediction of fusimotor activity preceding and actually initiating and accounting entirely for alpha-motoneuron activity in some movements has never been demonstrated, strong alpha-gamma coactivation compatible with some form of servo control was apparent during "automaton" walking in mesencephalic cats (35) and during respiratory movements of the intercostal muscles (13, 33). Strong alpha-gamma coactivation has been reported in humans during isometric contractions (40, 41) and rapid alternating movements (20). However, both reports suggested it was more compatible with functions other than a length-servo control operating at the spinal cord level. Much less alpha-gamma coactivation was seen during normal walking (31, 32) and chewing (9) movements in cats, with the effect in the latter limited simply to modifying the slopes of sensitivity to absolute stretch and velocity of stretch.

Functional muscle classification

Hagbarth, Wallin, and Lofstedt (20) pointed out that a given muscle may work in many different ways, depending on both its anatomical location and the task being performed at the moment. Cody, Harrison, and Taylor (9) observed that the same spindle had very different activity (and presumably different fusimotor input) for similar jaw movements performed during different activities, such as chewing versus lip licking. We report in this paper similar task-dependent spindle activity.

The great diversity of spindle-activity patterns, which we have observed in various hindlimb muscles during the single behavioral task of walking, probably arises from the very different roles played by the various muscles. Some muscles may be considered "prime movers" of the limb whose activity is and must be highly stereotyped to keep locomotion grossly coordinated (e.g., triceps surae, hamstrings, quadriceps). Other muscles may perform somewhat more variable supporting roles, such as stabilizing the nonmoving axis of a joint (e.g., gluteus minimus) as required by the variable demands resulting from ground contour, inertia during translational and radial accelerations,

prime mover fatigue, etc. Still other muscles may be quite dispensable to the ongoing movement and, therefore, available to the animal for strictly volitional variations (e.g., extensor digitorum longus) or to act as independent sense organs (e.g., possibly tenuissimus). Changing the behavioral task (or even different phases of a single task) could cause muscles to shift between classes, and it would be appropriate for their mode of proprioceptive control to shift also. It appears that voluntary and reflex events may be associated with spindle activity different from that seen during grossly similar movements under other circumstances (Figs. 3A, vs. 3B, 3A vs. 4, and 5A are suggestive but, admittedly, not compelling; see also Ref. 9). The existence of multiple, switched control systems converging on the fusimotor neurons would explain both the variety of patterns observed and their apparent instability in a given muscle.

Motor control systems

A number of motor control systems have been proposed or are derived from control theory; they each require different types of information to be fed back and, therefore, predict different patterns of observed spindle afferent activity.

The simplest role for the spindle would be as an unbiased detector of absolute muscle length, a role compatible with the activity described in this paper and in a previous paper by Cody, Harrison, and Taylor (9) for some presumed muscle spindle secondaries under some conditions. It has been suggested that spindle primaries might provide a stretch velocity signal, which could compensate for the phase delays in the efferent system (37), a function compatible with "high-frequency" afferents in jaw muscles (9), but not demonstrated in hindlimb. However, as discussed below, even these roles are not simple consequences of passive receptor properties and appear to be accompanied by patterned fusimotor input.

At the other extreme, Merton (28) proposed that the fusimotor-activated spindle could generate the entire control signal for the alpha-motoneuron via the Ia monosynaptic reflex pathway. While the available data does not support such a system, Stein (37) has pointed out that a significant length-servo assist to the alpha-motoneurons can

be achieved as long as the spindle is kept biased on during the active movement. Vallbo (41) discussed (unfavorably) the proposition that a spindle firing at a nearly constant rate during a muscle contraction (such as he described during voluntary isometric contractions in humans) would be capable of detecting and correcting for length errors in either direction; this would be consistent with the modest but persistent firing rates seen in many spindle primaries during active contraction of their muscles (see also Ref. 31). If only errors induced by increased load need be detected, then only gamma-dynamic activity would be required. Granit (18) has pointed out that such a control system normally operates silently, with little or no spindle activity apparent until the contracting muscle is abnormally stretched. Attempts to apply such perturbations during tracking tasks have revealed very little load-compensating gain in the monosynaptic stretch reflex (5). However, spinal reflex pathways are now known to be highly gated by descending and segmental activity (12, 15), and it is difficult to generalize across tasks.

The concept of a "stiffness" control signal using both spindle and GTO feedback to linearize mechanical properties of activated muscle has been proposed by Houk (22). However, our data suggesting modulation and variability of fusimotor tone would predict that such a system would be often unbalanced (since GTO sensitivity is presumably fixed) unless complex compensatory presynaptic gating were present.

One of the significant findings of the present and other recent studies is the apparent dissociation between alpha- and gamma-motoneuron activity under certain circumstances, raising doubts about the earlier concept of a tight alpha-gamma coactivating linkage (18). Alpha activity without apparent gamma activity has been demonstrated by Prochazka et al. (32). Isolated gamma activity has long been suspected to accompany arousal (18) and was recently shown to be enhancing stretch sensitivity during cyclical movements (9). We here report fusimotor initiation of spindle afferent activity in the absence of homonymous muscle contraction, passive stretch, or generalized arousal (see Figs. 8 and 9). Although it may be premature to describe these observations in

terms of a control system, there are certain elements in common among the various examples described. Under certain conditions the length of a muscle may be important, but active contraction of that muscle may be unnecessary or even counterproductive. For example, the hamstring muscles (see Fig. 2) must pause during swing to permit hip flexion and knee extension, but the ability to detect abnormalities in the speed of all the swing phase movements is critical to achieving proper foot placement and load transfer. Similarly, EDL spindles are well located to detect unstable footing conditions, resulting in abnormal plantar movements at the toes or ankle. Active contraction of EDL muscle at footfall would undesirably counteract toe grip; thus, isolated fusimotor activity may be employed to maintain spindle sensitivity during the yield phase muscle shortening (see Fig. 8). Similarly, shortening of gluteus minimus occurs primarily during swing when the muscle is not and should not be actively contracting. However, the ability to sense rotational movement at the hip is probably important in preparing the extensor and abductor muscles to accept the load transfer at footfall, and may account for fusimotor maintenance of spindle afferent activity (see Fig. 9). Even the remote, diffuse fusimotor activation accompanying the Jendrassik maneuver (7) may fall into this category because it effectively heightens the sensitivity of various muscle spindles to sudden trunk movements, which often accompany use of the arms to manipulate heavy objects.

It is of interest that these "isolated" fusimotor activations may be restricted to only a portion of the spindle population of a muscle (see Fig. 8). This would support the suggestion by Binder et al. (4) that the spindles in a given muscle should be viewed not as a homogeneous pool of sensors functioning in parallel, but rather as parts of a microorganization among the motor units comprising the muscle. Muscle spindles (and GTOs) might be predominantly influenced by only the small subset of motor units to which they are intimately mechanically connected (42) (see Fig. 9 and related text). Corollaries to such a hypothesis include the possibility of specialized central projections for those afferents back onto their "personal" alpha-motoneurons and the possibility that the activity of individual gamma-motoneuron collaterals and the spindle afferents they influence converge on interneurons capable of

deriving the extrafusal event to be detected. The latter hypothesis would permit the gamma-motoneurons to pursue divergent modes of activation of the spindles in a muscle (e.g., as in the EDL primaries, Fig. 8) without loss of information. It also suggests neural circuitry capable of deriving true muscle length under changing levels of fusimotor tone, a requirement suggested by the unsuitability of joint receptors to account for our kinesthetic sense (8). It may be possible to discern such microorganization in the muscle spindle system by correlating spindle responses with preceding local or single unit EMG activity and, conversely, correlating spindle action potentials with subsequent EMG recorded in various parts of the muscle.

Experimental determination of motoneuron activation

It would seem useful to develop muscle classifications meaningful to control theory and to correlate them with observed patterns of alpha- and gamma-motoneuron activity. However, there are a number of limitations to our ability to infer the timing of both alpha- and gamma-motoneuron activation from spindle activity, muscle length, and EMG records.

Cody, Harrison, and Taylor (9) observed that certain spindle activity patterns, while seeming to derive from strictly passive spindle properties, were, in fact, dependent on naturally occurring fusimotor modulation associated with the movement. Both the absolute length sensitivity of "low-frequency" receptors (presumably secondaries) and the high-velocity sensitivity of high-frequency (presumably primary) receptors were lost during deep anesthesia. It is now clear from acute physiological studies of spindle afferents that high dynamic index is a unique property of spindle primaries only for very small stretches of defferented spindles and may be lost (or enhanced) during more physiological magnitudes of movement and/or other states of fusimotor tone (21, 23). The spindle secondaries we observed responding proportionately to muscle length may do so only by responding as well to modulated fusimotor input. In fact, this is almost certainly the case since spindle primaries in the same muscles appear to be responding to gamma static activity, which should effect secondaries as well (27).

Separation of passive stretch- and fusimotor-induced spindle activity requires knowledge of the length of the spindle. Even

when muscle insertions and fiber orientation are appropriate for our implanted length gauges, the possibility of relative length changes within the muscle due to "squirming" between differentially activated muscle fibers severely limits the reliability with which we can quantitate spindle stretch sensitivity (42).

Studies of intrafusal muscle twitch properties and their effects on afferents predict highly variable and potentially large delays between the initiation and cessation of gamma-motoneuron activity and noticeable effects on spindle afferent activity. Single impulses from gamma static and even gamma dynamic motoneurons may initiate or modulate activity in some afferents within 10–15 ms, which then persists only 30–50 ms (6). However, some spindles are activated only by trains of fusimotor stimuli, which accumulate effects for 100–300 ms (even at tetanic frequencies), which may then require up to 500 ms to decay after the efferent volley ceases. The fast properties can account for rapid fusimotor modulation as seen during paw-shaking and reflex movements (Figs. 5 and 8); the slow properties may explain increased afferent sensitivity just following homonymous muscle contraction with presumed alpha-gamma coactivation, as suggested by Prochazka et al. (32) (see also Fig. 5B).

Even the alpha-motoneuron activation timing is subject to some uncertainty since it is derived from the EMG recordings rather than direct knowledge of the motoneuron polarization level. If the EMG voltage is zero, the motoneurons may be either just subthreshold or completely biased off. This may explain the persistent fusimotor activation apparent in hamstring muscle spindles during midswing when the muscle EMG shows a pause (see Fig. 2). This problem also causes difficulty in defining what is meant by isolated fusimotor activity, since one cannot completely rule out a concomitant but subthreshold alpha coactivation.

For all of the above reasons, we have found the active and passive categorization of spindle behavior to be an oversimplification, which must often be arbitrarily applied. Perhaps more systematic studies of instantaneous spindle stretch sensitivity will identify distinct patterns of fusimotor effects, which now appear as a continuum

from unmodulated background biasing to brisk, specific reflex actions.

Correlating muscle function and afferent control systems

Despite the previously discussed limitations, certain general patterns relating muscle function and spindle activity are suggested by the available body of data.

There appears to be a class of stereotyped, cyclical, nonballistic movements (e.g., walking, chewing, breathing); the associated prime-mover muscles typically display a consistent pattern of spindle afferent activity. Under these conditions, spindle secondaries seem generally to be signaling absolute muscle length. Primaries are usually alpha-gamma coactivated so as to be biased at, or at least near, levels resulting in low-level afferent activity during active muscle contraction. In the hindlimb, this suggests an ability to sense primarily increased load conditions, since inertia of the limb will translate a local obstruction into rapid and diffuse muscle stretches.

Circumstances attracting the animal's conscious attention to the level of muscle tone (e.g., lip licking (9), postural adjustments, voluntary contractions (40)), or causing arousal (e.g., Jendrassik maneuver (18), obstructions to gait (32)) generally result in higher fusimotor activity levels in both ac-

tive and passive muscles. Similarly, stimuli that elicit motor reflexes appear to result in rapid, brief, and possibly diffuse fusimotor activation of spindle secondaries and at least some primaries.

Isolated gamma-motoneuron activity (out of phase with alpha-motoneuron firing) has been apparent only in muscles that are involved in, or at least affected by, movements for which they are not, at the moment, the prime movers (e.g., temporalis during lip licking, gluteus minimus and EDL during walking). This suggests that, during such movements, these spindles may be utilized as pure sense organs whose sensitivity can be modulated independently of the contractile state of the muscles in which they reside.

It seems likely that we will come to describe much afferent and efferent activity in terms of control systems unlike those which, by their physiological and conceptual accessibility, have already attracted our attention.

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